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Relationships and Zoogeography of the Viperine Snakes (Family Viperidae)

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In the past year we had the opportunity to observe the behavior in captivity of two rare vipers, *Eristocophis mcmahoni* and *Pseudocerastes persicus*. On the death of these specimens we examined their skeletal and external anatomy. The data obtained lead to a new view of the relationships of *Pseudocerastes* and *Eristocophis*, whose generic status has been questioned by Anderson (1963). In the course of this work we also examined specimens of all other viperine genera. This assessment has resulted in the recognition of a new genus, the re-definition of others, and correlated speculation about the evolution and zoogeography of the vipers lacking loreal pits.

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The following is a list of viperine species examined. The first number refers to the number of specimens examined for that species; the number in parenthesis indicates the number of skulls examined.

7 *Adenorhinos barbouri**(3)	2 *Bitis heraldica* (1)
3 *Atheris chloroechis* (1)	10+ *Bitis nasicornis* (6)
2 *Atheris hindii**(1)	5 *Bitis peringueyi* (1)
1 *Atheris katangensis* (1)	1 *Bitis worthingtoni* (1)
10+ *Atheris nitschei* (2)	10+ *Causus defilippii*
10+ *Atheris squamiger* (5)	2 *Causus lichtensteini*
2 *Atheris superciliaris**(2)	6 *Causus resimus*
3 *Atractaspis aterrima*	10+ *Causus rhombeatus* (5)
10+ *Atractaspis bibroni*	10+ *Cerastes cerastes* (1)
1 *Atractaspis congica*	10+ *Cerastes vipera* (3)
4 *Atractaspis corpulenta*	10+ *Echis carinatus* (2)
3 *Atractaspis dahomeyensis*	5 *Echis coloratus* (1)
1 *Atractaspis engaddensis*	8 *Eristocophis mcmahoni* (2)
10+ *Atractaspis irregularis* (1)	7 *Vipera ammodytes* (3)
10+ *Atractaspis microlepidota* (1)	2 *Vipera aspis* (1)
1 *Atractaspis reticulata*	10+ *Vipera berus* (1)
2 *Azemiops feae*†(2)	10+ *Vipera lebetina* (1)
10+ *Bitis arietans*‡ (5)	10+ *Vipera persica* (1)
3 *Bitis atropos* (1)	10+ *Vipera russelli* (4)
10+ *Bitis caudalis* (3)	5 *Vipera ursini* (1)
3 *Bitis cornuta* (1)	3 *Vipera xanthina* (1)
10+ *Bitis gabonica* (3)	

* New name combination.

† Auffenberg (1963, p. 200) reported examining *Azemiops*. He informed us (personal communication) that the specimen he examined is UF 4030. This snake is *Psammodynastes pulverulentus* (Boie), Family Colubridae. The two animals noted above are USNM 84363 and 107534.

‡ We use the name *arietans* instead of *lachesis*, following Loveridge (1957, p. 301, footnote 174).

VIPERS OF THE PALAEARCTIC REGION

The Palaearctic viperines are not so morphologically diverse as the Ethiopian stocks, but they do have a considerable morphotypic span. *Azemiops*, from the eastern end of the range of the subfamily in Asia, has many primitive features. It approximately corresponds to the African genera *Causus* and *Atractaspis*. Like them, it has colubrid head scalation, but it differs significantly in many characters (Table 1). Unfortunately, nothing is known of its habits, ecology, or mode of reproduction. Judging from its morphology, *Azemiops* is nocturnal or crepuscular and semi-arboreal or terrestrial.

The other Palaearctic viperines are oviparous and viviparous (Mendelssohn, 1963), although definite data are lacking for *Eristocophis*. The four genera that we recognize (*Vipera*, *Eristocophis*, *Echis*, and *Cerastes*) are set off from the Ethiopian advanced vipers by the nature of the postorbital area of the skull. In all of them, the post-

TABLE 1.—COMPARISON OF CERTAIN CHARACTERS OF VIPERS
WITH LARGE HEAD SHIELDS

Character	*Atractaspis* (16)*	*Causus* (5)	*Azemiops* (1)
Postorbital......................	absent	present	present
Parietal posterior to postorbital.......	0	+	0
Premaxilla: dorso-posterior projection.	broadly triangular	narrow & pointed	?
Ectopterygoid with lateral flange.....	0	+	0
Fangs extend posteriorly beyond eye...	+	0	+
Mandibular teeth reduced to 2 or 3...	+	0	0
Skull modified for burrowing.........	+	0	0
Head distinct from neck.............	0	0	+
Head depressed....................	+	0	0
Nostril in contact with number of shields........................	2	3	1
Nostril in posterior nasal............	0	+	0
Supranasal invagination present......	0	0/+	0
Loreal present.....................	0	+	+
Pupil: round (R) or elliptical (E).....	R	R	E
Eye minute.......................	+	0	0
Dorsal scales smooth (S) or keeled (K)..	S	K	S
Apical pits.......................	0	+	0
Anterior ventral in contact with posterior chin shields.............	0	+	0
Ventrals..........................	178–370	143–155	170–190
Subcaudals........................	19–37	10–29	42–54
Scale rows........................	17–37	17–21	17
Habit............................	fossorial	terrestrial	?
Oviparous (Ov) or viviparous........	Ov	Ov	?

*=number of species: Laurent, 1950; Haas, 1952.

Fig. 32.   Skull of *Vipera russelli* (CNHM 22456).

orbital bone is a moderate-sized element that is firmly sutured poste-
riorly and medially to a lateral process of the parietal (fig. 32).   In
the three Ethiopian genera, the postorbital abuts on the parietal, but
does not form a common unit with it (fig. 33).   A further difference
is noted in the mandible: the splenial element is variously present or
absent in the Palaearctic taxa, but in the Ethiopian viviparous genera
its position is filled by an extension of the angular (fig. 34).

Of the advanced Palaearctic genera, *Vipera* is probably most like
the ancestral stock.   It has the most variable range of characters
(e.g., head shields, Table 3) and occupies a very extensive geographic
range (fig. 45) encompassing several ecological and climatic zones
(forest, steppe, desert).   Several of the species of *Vipera* have been
reviewed in recent years (for example, Kramer, 1961).

Kinkelin (1892, 1896) described *Provipera boettgeri* from a tooth
from a European Miocene deposit.   Cope (1892) strongly questioned
the naming of a new genus and species from a single tooth.   We con-
cur with Cope's opinion and believe that *Provipera* should be consid-
ered *incertae sedis*.

Vipera gedulyi (Bolkay, 1913) from the Pannonian deposits of
Hungary (lower Pliocene) appears to be correctly assigned to genus.

Fig. 33.   Postorbital-parietal region of *Bitis arietans* (CNHM 11006).

Other European fossil forms such as *Laophis crotaloides* (Owen, 1857) are probably viperines, but their status needs elucidation based on re-examination of the fossil specimens.   Further discussion of the genus *Vipera* is given below in relation to the status of *Pseudocerastes* and *Eristocophis*.

Cerastes and *Echis* are apparently closely related.   They are conveniently distinguished from the other Palaearctic genera by their lack of a splenial bone.   In addition to common general internal anatomy, a striking external feature that they share is the oblique lateral rows of scales with serrated keels.   Many of the characteristics of scutellation that distinguish *Cerastes* from *Echis* (Table 2) are probably related to the loose sand habitat and the behavior of *Cerastes*.   Head shape, eye size, and length of tail in *Cerastes* may be similarly correlated.   Many of these gross anatomical and scute modifications are also found in *Bitis peringueyi* and *Eristocophis mcmahoni*, both dune dwellers.   However, there are other differentiating characteristics not so clearly related to ecology (single subcaudals, unilobate anterior process of the atlas intercentrum).   That

CAUSUS

ATRACTASPIS

AZEMIOPS

VIPERA

ERISTOCOPHIS

ECHIS
CERASTES

BITIS
ATHERIS
ADENORHINOS
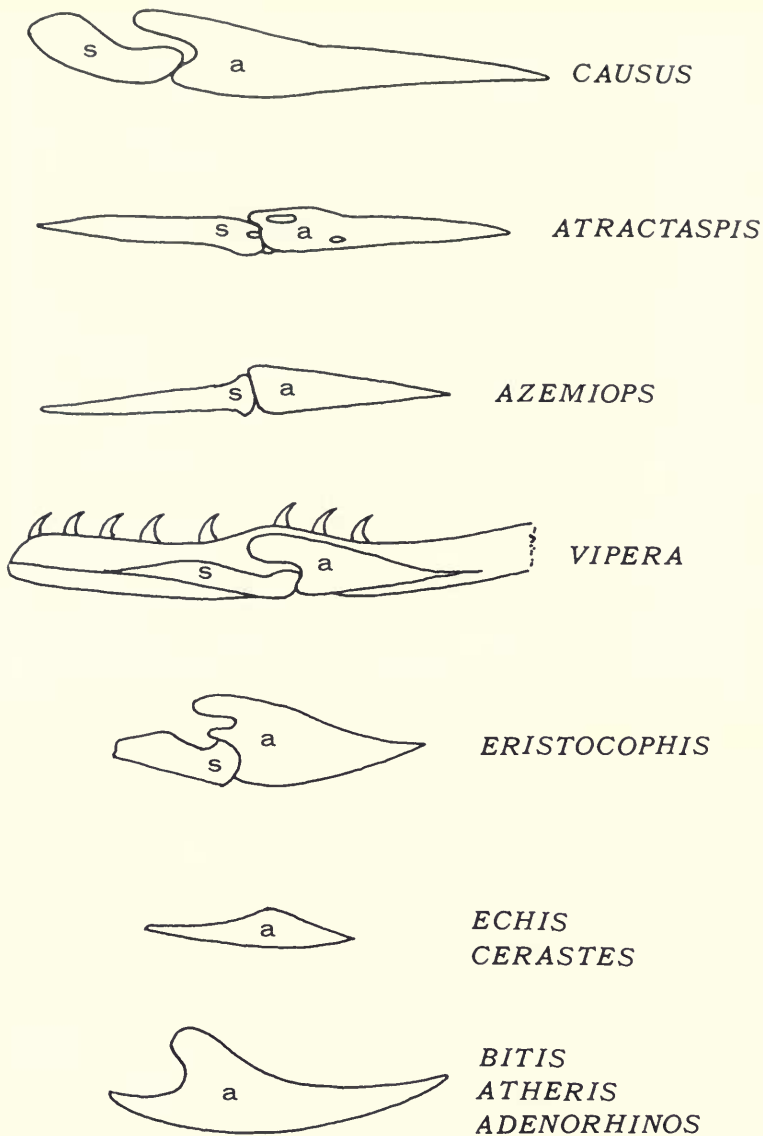
a = angular
s = splenial

FIG. 34.   Splenial and angular arrangements of viperid genera.

166

Echis and *Cerastes* each have two species appears significant to us in indicating a respectable history for each as a distinct stock. Although there is considerable variation within some of the taxa (e.g., head muscles of *Cerastes cerastes*, Kochva, 1962), there are no obvious gradual transitions among the four taxa. We therefore recognize the two genera.

TABLE 2.—COMPARISON OF CERTAIN CHARACTERS OF
ADVANCED VIPERS OF THE PALAEARCTIC REGION

Character	*Vipera*	*Echis*	*Cerastes*	*Eristocophis*
Dorso-posterior projection of premaxilla	pointed	pointed	pointed	spatulate
Atlas: antero-ventral process	bilobed	unilobed	bilobed	unilobed
Atlas with epizygapophysial spine	+	+	+	0
Axis: posterior lobe of antero-ventral process	bilobed	bilobed	absent	absent
Splenial present	+	0	0	+
Supranasal sac	+(4) 0(4)	0	0	+
Nasal in contact with first supralabial	+(7) 0(1)	+(1) 0(1)	0	0
Supralabials	6–14	10–12	10–15	14–16
Infralabials in contact with anterior chin shields	3–5	3–4	3	2–3
Numerous small gulars	0	+	+	+
Gulars: smooth or keeled	S	S	K	K
Scale rows in "rings" (as in fig. 37)	0	0	+	+
Dorsal scales oval (Ov) or squarish (Sq)	Ov	Ov	Sq	Sq
Dorsal scale rows	19–33	27–37	23–35	23–26
Lateral scales serrated	0	+	+	0
Lateral scales forming a sharp, oblique angle to dorsal scales	0	+	+	0
Ventrals: smooth (S) or keeled (K)	S	S	K	K
Ventrals	120–180	132–205	102–165	140–148
Subcaudals: single (S) or paired (P)	P	S	P	P
Subcaudals: smooth (S) or keeled (K)	S	S	K	S
Subcaudals	20–64	21–48	18–42	29–36

STATUS OF THE GENUS *PSEUDOCERASTES*

Boulenger (1896) distinguished *Pseudocerastes* from *Vipera*, noting that *Pseudocerastes* has the nasal scale separated from the rostral by small scales whereas *Vipera* has the nasal in contact with the rostral or separated by a large naso-rostral shield. Three species of *Vipera* (*lebetina*, fig. 35, D; *xanthina*; *russelli*) have the nasal in contact with the rostral and four species (*berus*, *ursini*, *aspis*, *ammodytes*) have them separated by a large naso-rostral shield. *Pseudocerastes* does have small scales separating the nasal from the rostral (fig. 35, B).

Fig. 35. A–B, *Vipera p. persica* (MHNP 57–66); C–D, *Vipera lebetina* (CNHM. 65219)

168

Pseudocerastes was further distinguished from *Vipera* by Smith (1943), who found that *Pseudocerastes* has a supranasal sac whereas *Vipera* lacks this sac. There is an invagination beneath the supranasal scales in three of the seven species of *Vipera* we examined. This proto-sac is present in varying degrees in *V. lebetina* (fig. 35, D), *V. xanthina,* and *V. russelli.* The sac is deepest in *Pseudocerastes.*

There are three characters in which *Pseudocerastes* and *Vipera* differ (Table 5): the scales between the nasal and the rostral, scales between the nasal and the first supralabial, and supraocular "horns." Similar ranges of variation in the scute relations of the nasal were found in *Bitis* (Table 9). There are enlarged supraocular horn-like scales in *Pseudocerastes* (fig. 35, B). The parallel development of supraocular horns in desert or arid land species of other viperid genera (*Crotalus, Bitis, Cerastes*) indicates that the structures possess some ecologically related selective advantage. Cope (1900, p. 1130) and Parker (1963, p. 85) suggested that they may serve a camouflage purpose. However, there is no reason to consider these and similarly specialized scales on the snout in *Vipera* (*ammodytes* and *aspis*) and *Bitis* (*nasicornis* and *gabonica*) as other than species characteristics.

The species of *Vipera* show a graded reduction in the number of large dorsal shields of the head from *berus, ursini,* and *aspis* to *lebetina* (fig. 35, C) and *ammodytes* (Table 3). Most of the specimens of the eastern subspecies of *Pseudocerastes persicus* (*P. p. persicus:* 12 or 15 examined) have an enlarged supranasal shield. Direct comparison of specimens of *Pseudocerates persicus* and the species of *Vipera* with fewest enlarged head scales shows a marked resemblance between the scalation of *persicus* and *lebetina* (fig. 35).

Kochva (1962) examined the head musculature of numerous snakes, including eight species of *Vipera.* He stated that "The head musculature of *Pseudocerastes* conforms closely with typical members of the genus *Vipera.*"

With the marked differences between *Eristocophis* on the one hand and *Pseudocerastes* and *Vipera* on the other (Table 7), and the negligible differences between *Pseudocerastes* and some species of *Vipera* (Tables 3, 5 and 7), recognition of *Pseudocerastes* as a distinct genus does not seem warranted. We therefore synonymize *Pseudocerastes* with *Vipera.*
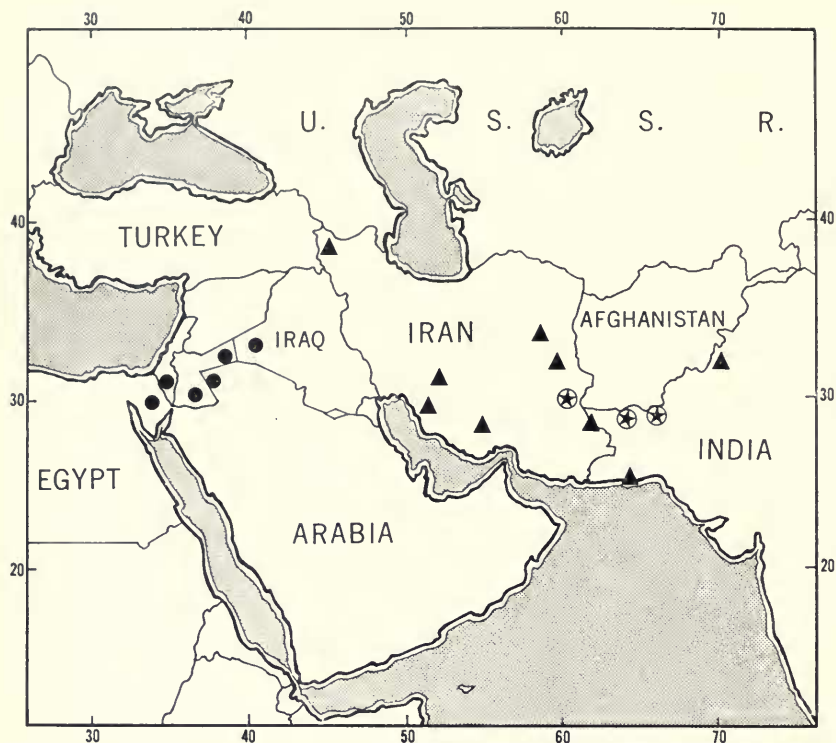
FIG. 36. Distribution of *Eristocophis* and *Vipera persica*. Star=*E. mcmahoni*; dot=*V. p. fieldi;* triangle=*V. p. persica.*

TABLE 3.—ENLARGED HEAD SHIELDS IN *VIPERA* AND
"*PSEUDOCERASTES*" SPECIES

Species	Parietal	Frontal	Supraocular	Supranasal
P. persicus	0	0	0	+
V. lebetina	0	0	0	+
V. ammodytes	0	0	+	0
V. russelli	0	0	+	+
V. xanthina	0	0	+	+
V. aspis	0	0/+	+	0/+
V. berus	0	+	+	+
V. ursini	+	+	+	+

TABLE 4.—GEOGRAPHIC VARIATION OF CERTAIN CHARACTERS
OF *VIPERA PERSICA*

	V. p. persica	*V. p. fieldi*
Midbody scale rows	23–24(23.3)14	21–23(21.8)5
Ventrals: ♂	144–158(151.0)9	134 1
Ventrals: ♀	145–155(149.0)5	134–138(136.7)3
Subcaudals: ♂	41–48(44.6)9	35 1
Subcaudals: ♀	38–43(40.8)5	36–38(37.0)3
Scales in ocular ring*	13–23(18.3)32	14–18(15.8)12
Scale rows between nasal and rostral*	1–2(1.8)32	2 10
Supranasal scales*	1–2(1.2)30	1–2(1.9)10
Tail length relative to total length: ♂	0.116–0.155(0.128)7	0.116 1
Tail length relative to total length: ♀	0.121–0.132(0.126)5	0.105–0.118(0.111)3

* each side of head counted as one to determine mean.

TABLE 5.—COMPARISON OF CERTAIN CHARACTERS OF
PSEUDOCERASTES AND *VIPERA*

Characters	*Pseudocerastes*	*Vipera*	
Postorbital contact with frontal	0	0 (1)*	+ (4)
Basi-occipital spine	+	stump (1)	+ (4)
Prefrontals in contact	0	0 (4)	+ (1)
Supranasal sac	+	0 (4)	+ (3)
Scales between nasal and rostral	1–2 small	0 (3)	1 enlarged (4)
Scales between nasal and first supra-labial	1[17] 0/1[1] 0[1]**	0 (7)	
Supraocular "horns"	+	0 (7)	
Enlarged head shields: supranasal	+	0 (1)	+ (6)
supraocular	0	0 (1)	+ (6)
parietals	0	0 (6)	+ (1)
frontal	0	0 (6)	+ (1)
Premaxilla: dorso-posterior projection pointed (as in fig. 39, B)	+		+ (5)
Gulars smooth	+		+ (7)
Ventrals smooth	+		+ (7)
Dorsal scale rows oblique	+		+ (7)
Slender splenial present	+		+ (7)

*= (species examined)
**=[specimens examined]

STATUS OF THE NAMED FORMS OF THE GENUS *"PSEUDOCERASTES"*

Schmidt (1930) distinguished *Pseudocerastes fieldi* from *P. persicus* and *P. bicornis* by three characters: 21 scale rows, two series of scales between nasal and rostral, and lower number of ventrals and subcaudals. Table 6 gives the frequency distribution of these characters over the major geographic zones occupied. Table 4 gives all characters observed to have some geographic variation between the eastern and western population samples.

Only the ventral counts and relative tail length of females have no overlapping range of variation (Table 4). The other observed characters have some degree of overlap at varying degrees of frequency (Table 6).

There are no significant differences between the two sampled populations east of the Zagros Mountains, but significant differences appear between the populations west and east of the Zagros Mountains. Is there complete genetic isolation of animals on either side of this mountain range? Specimens are known from an altitude of 5000 feet in India (Smith, 1943), and it thus appears likely that the Zagros mountain range could be penetrated, allowing some gene flow. With the large number of their characters that have overlapping ranges of variation and so few characters having no overlap, we regard these western and eastern populations as subspecies. We have directly compared the holotypes of *persica* and *fieldi* and have no doubt about the closeness of their relationship to each other; they are identical in general appearance.

Pseudocerastes bicornis Wall (1913) was described from Waziristan. The only difference between *P. bicornis* (only the anterior one-fourth of the body present in the single known specimen) and *persica* is that *bicornis* has 21 scale rows where the specimen ends (Smith, 1943), whereas *persica* has 23 to 25 scale rows at mid-body. Wall (1928) and Smith (1943) both reported that anterior to the break there are 24 scale rows in the holotype of *bicornis*. Smith suggested that this specimen might be an aberrant individual or a northern form of *persica*. Examined specimens of *persica* from northern, western, and eastern Iran and western Pakistan have 23 or 24 scale rows at mid-body. There is no justification for recognizing these eastern specimens as representing a distinct taxon, or for assuming that this eastern population is genetically isolated from the western ones. The examples of western *persica* are from localities at least as dis-

Table 6.—FREQUENCY DISTRIBUTION OF CERTAIN CHARACTERS OF *VIPERA PERSICA*

Dorsal scale rows

	21	22	23	24
Southwestern Asia	2	2	1	
Western Iran			2	1
Eastern Iran, Pakistan			5	2
Iran (no other data)			3	1

Series of scales between rostral and nasal

	1	1–2	2
Southwestern Asia			5
Western Iran	1		4
Eastern Iran, Pakistan	1	1	6
Iran (no other data)			4

Ventrals

	134	136	138	144	145	147	148	149	151	153	154	155	158
Southwestern Asia	2	1	2										
Western Iran					1	1					1		
Eastern Iran, Pakistan				1		1	1	1	2	1			
Iran (no other data)						1					1	1	1

Subcaudals

	35	36	37	38	40	41	42	43	44	46	47	48
Southwestern Asia	1	2	1	1								
Western Iran					1	1		1			1	
Eastern Iran, Pakistan							2	1	2	1		
Iran (no other data)				1		1				1	1	

Scales in ocular ring*

	14	15	16	17	18	19	20	21	22	23
Southwestern Asia	4	2	3	4	1					
Western Iran					5	2	1			
Eastern Iran, Pakistan			2	1	3	7	2			1
Iran (no other data)		1	1	2	1	2				

Supranasal scales

	1	1–2	2
Southwestern Asia		1	4
Western Iran	3		
Eastern Iran, Pakistan	6		2
Iran (no other data)	3		1

* each side of head counted once.

173

tant from each other as the type locality of *bicornis* is from eastern Iranian and western Pakistan localities of *persica*. There are no significant morphological differences between samples from Iran. *Pseudocerastes bicornis* falls within the range of morphological variation of the widely scattered samples of Iranian *persica*. We therefore synonymize *Pseudocerastes bicornis* with *Vipera persica*.

Vipera persica (Duméril and Bibron)

Diagnosis.—Postorbital bone narrow (fig. 32); supraocular "horns" present (fig. 35, B); keels of lateral scales not serrated.

Vipera persica persica (Duméril and Bibron). Figure 35, A and B.

> *Cerastes persicus* Duméril and Bibron, 1854, Erp. Gén., 7, p. 1443, pl. 78b, fig. 5—Persia.
>
> *Vipera persica*, Jan, 1859, Rev. and Mag. Zool., p. 153.
>
> *Pseudocerastes persicus*, Boulenger, 1896, Cat. Sn. Brit. Mus., 3, p. 501.
>
> *Pseudocerastes bicornis* Wall, 1913, Pois. Sn. India, p. 64—Khajieri Kach above Gwaleri Kolal in the Gomal Pass, Waziristan.

Total lengths: males 220–848 mm. (7); females 484–702 mm. (5).

Distribution.—Central Asia, east of the Zagros Mountains and south of the Caucasus, eastward into West Pakistan (fig. 36).

Material examined.—IRAN (LM 1084–85, 9299; MNHP 4027-holotype): Azerbaijan Province; Khoi (CNHM 109993). Khuzistan Province; Aminabad (CNHM 20933), Binak, at foot of Kuh-i-Bang (CAS 86633). Laristan Province; road between Bender-Abbas and Lar, 50 km. from Lar (MNHP 57–66). Khurasan Province; Arusan (NHMW 17225). Baluchistan, Ziarat (NHMW 17150, 17226).

WEST PAKISTAN: La Bela District, Ormara (SAM 862), near Ormara (RSM 2 unnumbered).

IRANIAN-PAKISTAN BORDER: Baluchistan, Kacha (BMNH 1937.-3.1.11), Marignli or Maryuli (BMNH 1937.3.1.12).

Vipera persica fieldi (Schmidt), new combination

> *Pseudocerastes fieldi* Schmidt, 1930, Field Mus. Nat. Hist., Zool. Ser., 17, p. 227, pl. 2, fig. 2—Bair Wells, Jordan.

Total lengths: male 715 mm.; females 582–667 mm. (3).

Distribution.—Extreme western Asia (figure 36).

Material examined.—CENTRAL SINAI: "White Ridges," 9 miles south of Hassana and about 29 miles north of Nekhl (Flower, 1930—not seen).

ISRAEL: Negev, Darbes Sultan, 3 miles east of Mount Quatrin (NHMW 14783).

JORDAN: Bair Wells (CNHM 11061–62, holotype and paratype), Um Wu'al (CNHM 11063, paratype).

SAUDI ARABIA: W. Sirhan (BMNH, not seen—data furnished by A. G. C. Grandison).

IRAQ: Rutba (CNHM 19583–84).

STATUS OF THE GENUS *ERISTOCOPHIS*

Eristocophis has been distinguished from the genus *Pseudocerastes* on the basis of the arrangement of the lateral scales and keeled ventrals (Smith, 1943, p. 480) and related to *Pseudocerastes* in having a supranasal sac (op. cit., p. 19). The genera were synonymized by Anderson (1963, p. 472).

The supranasal sac does not necessarily reflect immediate common descent. In the material examined, the sac or a definite invagination beneath the supranasal scales is present in the nine species of *Bitis* (Table 9; Parker, 1932), three of the four species of *Causus* (Table 1; Lynn, 1935), and four of the eight species of *Vipera* (including *V. persica;* Table 5). Presence of such structures in groups as diverse as *Causus*, *Bitis*, and *Vipera* strongly implies an ancient shared genetic capacity in the viperine line or completely independent origin in each of these stocks.

The arrangement of the dorsal and lateral scales is very different in *Eristocophis* as compared to *V. persica*. *Eristocophis* has dorsal and lateral scales arranged in rings (fig. 37, A) and the scales are short, whereas in *V. persica* they are elongate and arranged in oblique rows (fig. 35, A, B) as in other species of *Vipera* (fig. 35, C, D). *Eristocophis* is most similar to *Cerastes* in this character (Table 2).

Eristocophis has a most peculiar premaxilla, for the dorso-posterior process is concave and spatulate with an expanded posterior "paddle" (fig. 39, A). We have not seen this osteological character in any other genus of the family. Its function escapes us. It apparently is not needed for sand burrowing. After this snake sinks into the sand, it rotates its head on the longitudinal axis covering its head
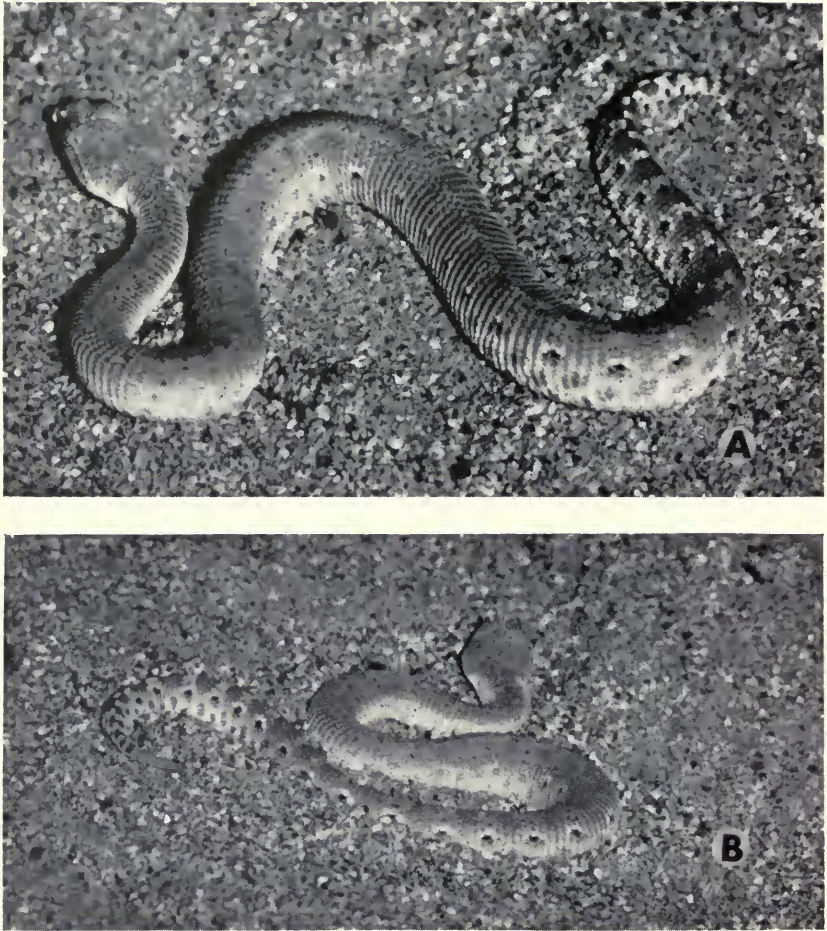
Fig. 37. Living *Eristocophis mcmahoni* (CNHM 140309).

with sand, and does not use its snout for burrowing (fig. 38, B). We believe that the form of the premaxilla has no functional relation to the elaborate snout scalation.

In addition, *Eristocophis* differs from *V. persica* in a reduced basi-occipital spine, processes on the atlas, absence of "horns" over the eyes, keeled ventrals, and a relatively shorter tail (Table 7). *Eristocophis*' striking span of locomotion (film of CNHM 140309 in Chicago Zoological Society film library), viz., sinking in sand (fig. 37), side-winding, rectilinear, serpentine, and climbing in bushes using a pre-hensile tail, is perhaps unique among the Viperinae. Because of the

Fig. 38.   Living *Eristocophis mcmahoni* (CNHM 140309).

differences in osteology, head and body scalation, and proportions (Tables 2 and 7), plus the range of locomotion, we subscribe to the generic distinction of *Eristocophis* from *Vipera*.

Eristocophis Alcock and Finn

Eristocophis Alcock and Finn, 1896, J. Asiat. Soc. Bengal, **65**, p. 564—type species *Eristocophis mcmahoni* Alcock and Finn.

TABLE 7.—COMPARISON OF CERTAIN CHARACTERS OF *ERISTOCOPHIS*, *PSEUDOCERASTES* AND *VIPERA*

Character	*Eristocophis*	*Pseudocerastes*	*Vipera*
Premaxilla: dorso-posterior projection	spatulate	pointed	pointed
Basi-occipital spine	stump	long	long(4) stump(1)*
Angular	broad	narrow	narrow
Splenial	oblong	splint	splint
Epizygapophysial spine on atlas	0	+	+
Antero-ventral intercentral process of atlas	unilobed	bilobed	bilobed
Supraocular horns	absent	present	absent
Gulars	keeled	smooth	smooth
Ventrals	keeled	smooth	smooth
Dorsal scale rows	rings	oblique	oblique
Dorsal scales	squarish	ovate	ovate
Prehensile tail	present	absent	absent
Relative tail length to total length	0.085–0.104(0.094)8	0.105–0.155(0.123)17	

* number of species

178

Generic diagnosis.—A viperine with the dorsoposterior projection of premaxilla spatulate (fig. 39, A); dorsal scale rows in straight rings (fig. 37, A); ventrals and gulars keeled; "butterfly scaled" snout region above rostral (fig. 38, A).

Description.—Skull: posterior projection of premaxilla spatulate (fig. 39, A); prefrontals not in contact with each other; postorbital not in contact with frontal; basioccipital spine a reduced stump. Splenial broad, rather rectangular (fig. 34). Atlas lacking epizygapophysial spine and having the antero-ventral intercentral process unilobate. Head distinct from body and covered with small scales; nasal separated from rostral by a greatly enlarged scale (fig. 38, A) and separated from first supralabial by a small scale; gulars keeled; one enlarged pair of chin shields. Body with keeled, short dorsal and lateral scales; keels unserrated; body scales arranged in straight rings; ventrals with lateral keels. Prehensile tail short, with paired, smooth subcaudals.

Eristocophis mcmahoni Alcock and Finn. Figures 37, 38, 39A.

Eristocophis mcmahoni Alcock and Finn, 1896, J. Asiatic Soc. Bengal, **65**, p. 564—type locality: desert south of the Helmand, Baluchistan.

Pseudocerastes latirostris Guibé, 1957, Bull. Mus. Paris, (2) **29**, p. 140, fig.— Tasuki, 120 km. from Zabol on route to Zahédan, Iran.

Pseudocerastes mcmahoni, Anderson, 1963, Proc. Calif. Acad. Sci., **31**, p. 472.

Taxonomic notes.—Anderson (1963) stated that Dr. Jean Guibé compared the holotype of *Pseudocerastes latirostris* with a description of *Eristocophis mcmahoni* and they both believe the forms are synonymous. Dr. Guibé was kind enough to send us the holotype of *P. latirostris* and we find this snake identical with the other specimens of *E. mcmahoni* examined.

Diagnosis.—Same as generic diagnosis.

Description.—In addition to the generic description: supranasal sac present; two scales over supranasal sac; wing-like scales above rostral; scales in 23 to 26 scale rows at mid-body; supralabials 14–16; infralabials 16–19; scales in ocular ring 16–22; anal plate single. Ventrals: males 140–144 [mean 141.5 (3)], females 142–148 [mean 145.6 (5)]. Subcaudals: males 33–36 [mean 34.7 (3)], females 29–31 [mean 29.6 (5)]. Relative tail length to total length: males 0.100–0.104 [mean 0.102 (3)], females 0.085–0.092 [mean 0.089 (5)]. Total length: males 221–390 mm. (3), females 283–715 mm. (5).

Distribution.—The sand dunes of the Dasht-i-Margo Desert, which occupies southwestern Afghanistan, eastern Baluchistan, Iran,

and north Baluchistan, West Pakistan (fig. 36). Krishna and Dave (1956) report this species from the Rahasthan Desert, India (north-western portion of Jaisalmer district).

Material examined.—IRAN: Baluchistan; Tasuki, 120 km. from Zabol on route to Zahédan (MHNP 57–62, holotype of *latirostris*).

WEST PAKISTAN: Baluchistan (AMNH 92722–23; CNHM 140280, 140309); Chagai District, Nushki (SAM 832), near Chagai (RSM unnumbered). Baluchistan, south of Helmand (BMNH 96.12.22.14).
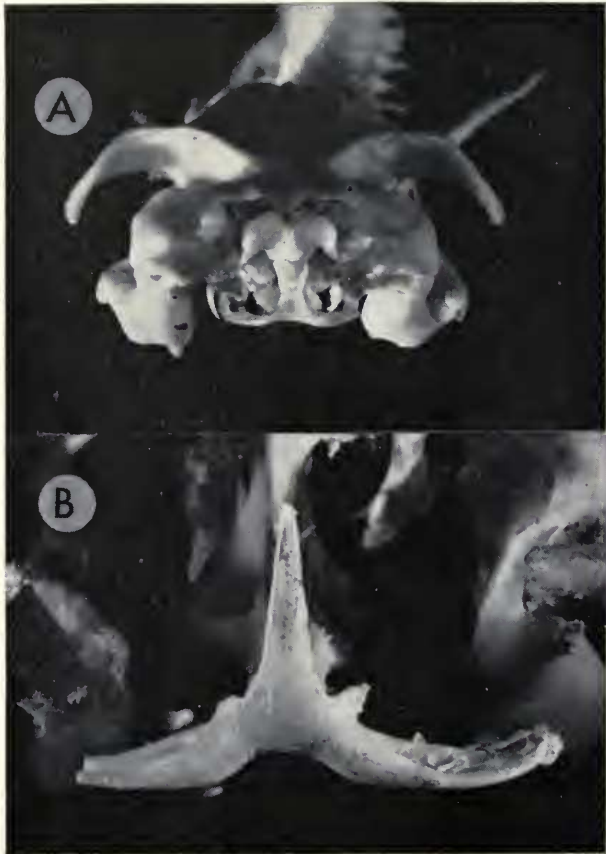

FIG. 39. Premaxilla of (A) *Eristocophis mcmahoni* (CNHM 140280) and (B) *Vipera russelli* (CNHM 22456).

VIPERS OF THE ETHIOPIAN REGION

Two groups of vipers are sympatrically distributed in the Ethiopian region. One group is oviparous and has large, smooth head plates (as in Colubridae), a round pupil, and both splenial and angular elements in the mandible. This group consists of the genera *Causus* and *Atractaspis*, and both have extensive ranges in Africa (fig. 44). Member species within either genus are so similar to each other and the genera so morphologically different (Table 1) that the generic separation has been consistent in all of the literature (Boulenger, 1896; Klemmer, 1963). Their various similarities to the Asiatic genus *Azemiops* (Table 1) are countered by several differences that make close relationship rather unlikely. Actually, *Atractaspis* shares more of the examined characters with allopatric *Azemiops* than with sympatric *Causus* (Table 1).

Atractaspis is well adapted for a fossorial mode of life, as shown by the shape of the skull, relative enlargement of certain head shields, minute eye, etc. (Laurent, 1950). The terrestrial genus *Causus* is much less specialized in morphology, but its markings, snout shape and diet of toads make it an intriguing convergence to the genus *Heterodon* of North America (Bogert, 1940).

The second group of Ethiopian vipers (Table 8) is viviparous so far as known, and has small, keeled head scales, elliptical pupils, and lacks a splenial element in the mandible. This second group has usually been divided into two genera which differ in certain morphological characters (e.g., subcaudals paired or single, and tail prehensile or not [Boulenger, 1896; de Witte, 1962]) and in their basic ecological adaptation (terrestrial or arboreal). The terrestrial forms have usually been assigned to *Bitis* and the arboreal forms to *Atheris*. Two species (*hindii* and *superciliaris*) have been considered members of the Palaearctic genus *Vipera* (Boulenger, 1896; Klemmer, 1963) or members of the genus *Bitis* (Kramer, 1961).

We examined 16 of the 19 currently recognized species of these vipers (Table 9). Nine species have a large flange on the ectopterygoid (as in figs. 42 and 43), a broad postorbital (as in figs. 33 and 43), and a well developed supranasal sac. These species are all terrestrial and span a wide range of habitats, from the equatorial tropical forests (*nasicornis*, *gabonica*), into the southern African arid regions (*caudalis*, *cornuta*), including desert dunes (*peringueyi*) (Brain, 1960). Despite such diverse ecological adaptations they all have the ectopterygoid flange, a broad postorbital, and a supranasal sac. We, therefore, interpret these characters as reflecting close phylogenetic

relations and recognize *peringueyi, caudalis, cornuta, atropos, heraldica, arietans, gabonica, nasicornis,* and *worthingtoni* as species belonging to the genus *Bitis* (genotype—*Bitis arietans*).

Pseudocerastes (here, *Vipera persica*) was reported to be related to *Bitis* (Parker, 1932) and its affinity to *Bitis* was based primarily on the presence of a supranasal sac in both genera. However, the weight of the osteological evidence indicates that the occurrence of a nasal sac in *Vipera persica* (and *Eristocophis*) is a case of parallelism.

A fossil snake from the Pontian Hipparion fauna of Spain was identified as *Bitis* sp. by Piveteau (1927). This fauna is now considered early Pliocene (A. S. Romer, personal communication). This is the only record of the genus not from the Ethiopian Region. Dr. Robert Hoffstetter of the Institut de Paléontologie, Museum National d'Histoire Naturelle, Paris, examined this specimen at the Instituto Goya, Zaragoza, Spain. He informed us (personal communication) that this fossil snake is a member of the family Colubridae, having a "maxillaire supérieur de type Colubridé."

Six examined species of the viviparous Ethiopian vipers (Table 9) lack the flange on the ectopterygoid (as in fig. 42), have a relatively narrow, long postorbital, and no supranasal sac. They are all from tropical Africa. These six species inhabit two ecological zones, terrestrial (*hindii, superciliaris*) and arboreal (*nitschei, squamiger, chloroechis, katangensis*). Because of correlation of the type of ectopterygoid, absence of a supranasal sac, and a narrow postorbital (Table 9), we believe these six species (*hindii, superciliaris, nitschei, katangensis, squamiger, chloroechis*) are closely related. We assign them to the genus *Atheris* (genotype: *Atheris squamiger*).

Our interpretation of the phylogeny of this *Bitis-Atheris* complex appears in figure 40.

Three presently recognized taxa, *Bitis inornata, Atheris ceratophorus* and *Atheris hispidus,* were not examined. From the external morphological descriptions and illustrations of these forms their generic assignments are probably correct.

Another morphotype is represented by the species *barbouri*. The ectopterygoid of this viper has a flange (as in *Bitis*) but lacks a distinctive spine, and has a medial anterior process (fig. 42). A narrow postorbital is present as in *Atheris*. The posterior area of the nasal shield has an exposed semicircular cavity (fig. 41, C). In no way does this structure appear like the supranasal sacs of *Bitis, Causus,*
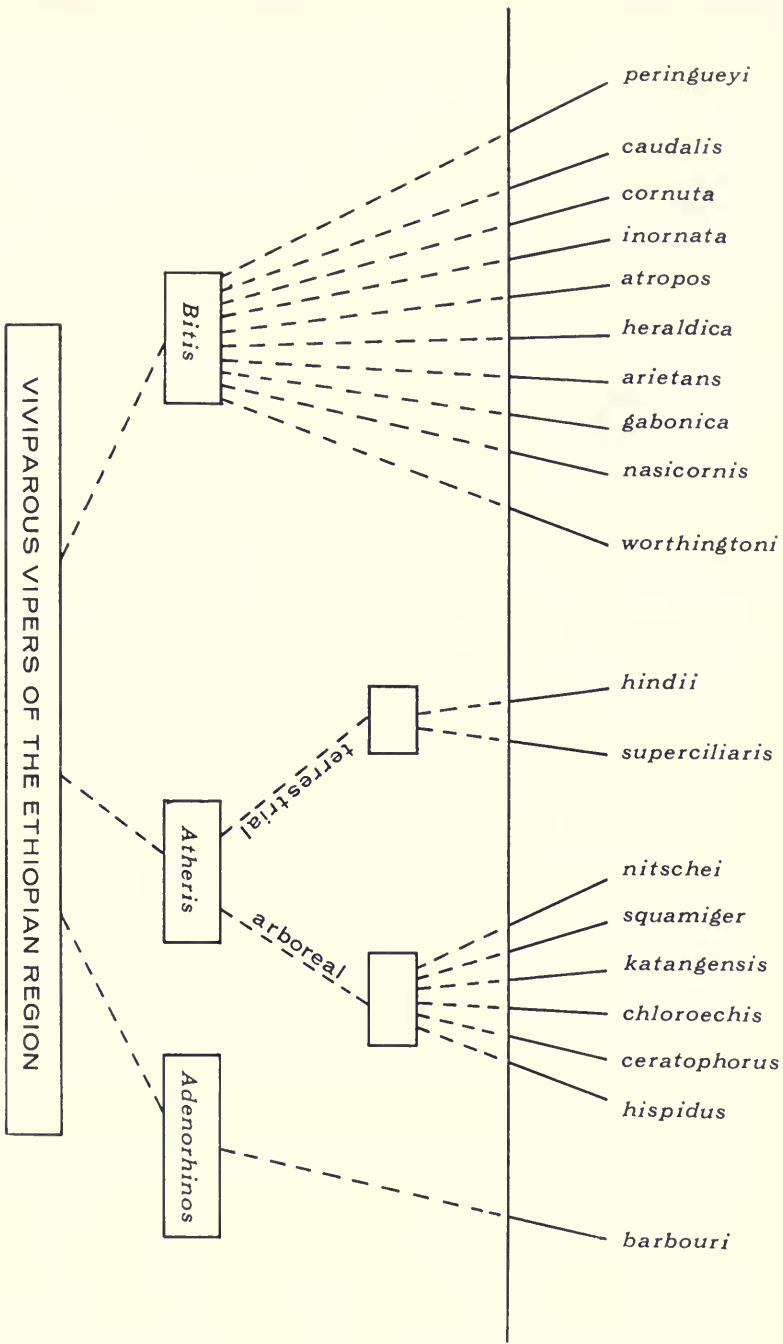
FIG. 40. Hypothetical phylogeny of viviparous vipers of the Ethiopian Region.

VIVIPAROUS VIPERS OF THE ETHIOPIAN REGION

Bitis

peringueyi
caudalis
cornuta
inornata
atropos
heraldica
arietans
gabonica
nasicornis
worthingtoni

Atheris

terrestrial

hindii
superciliaris

arboreal

nitschei
squamiger
katangensis
chloroechis
ceratophorus
hispidus

Adenorhinos

barbouri

183

and some *Vipera*. The presence of a subcutaneous compound mucus secreting nasal gland in this species is unique in the viperines. The supratemporal is relatively greatly distant from the postorbital (Table 8), and the intermediate parietal region has a distinct bulbous area. The head scales are different from all the species of *Bitis* and *Atheris* (fig. 41; Table 8). The head shape and scalation are superficially very similar to some slug-eating snake genera of other families (figs. 41, A, B). *Bitis* and *Atheris* feed on terrestrial and arboreal animals such as lizards, rodents, shrews, frogs, birds, and dikdik (Bogert, 1940, p. 100; Fitzsimons, 1962, pp. 338–351; Loveridge, 1933, pp. 275–276, 1942, pp. 311–314, 1953, p. 295, 1955, p. 194; Werner, 1897, p. 401). Loveridge (1933, p. 278) found an earthworm in the gut of one *barbouri* among several that were "dug up" when hoeing for planting. This species possibly represents a radiation of the viviparous Ethiopian vipers toward a subterrestrial life, and it is apparently adapted for feeding on soft-bodied animals. We believe this species merits generic distinction from *Bitis* and *Atheris* because of its many morphological differences which, combined with the few ecological observations, suggest radically different feeding habits and habitat.

TABLE 8.—COMPARISON OF CERTAIN CHARACTERS IN
BITIS, *ATHERIS*, AND *ADENORHINOS*

| Character	*Bitis* 9 species	*Atheris* 6 species	*Adenorhinos* 1 species
Ectopterygoid with flange	+	0	+
Ectopterygoid flange with spine	+	0	0
Ectopterygoid medial anterior process	0	0	+
Parietal bulbous laterally	0	0	+
Distance between supratemporal and postorbital/length of supratemporal	0.33–0.40	0.50–0.60	1.00
Distance between supratemporal and postorbital/frontal suture	0.20–0.33	0.25–0.33	1.14
Nasal in contact with preoculars	0	0	+
Nasal depression	0	0	+
Subcutaneous nasal gland	0	0	+
Position of nostril in nasal	Center-posterior	Anterior 1/3-posterior	Anterior border
Temporals: smooth (S) or keeled (K)	K	K	S
Temporal: one anterior enlarged	0	0	+
Temporal: one posterior enlarged	0	0	+
Number of supralabials in contact with suboculars	0	0–1	3
Supralabials	10–18	7–13	5–6
Infralabials	11–21	8–13	5
Paired enlarged chin shields	1	1 or 5–6	2
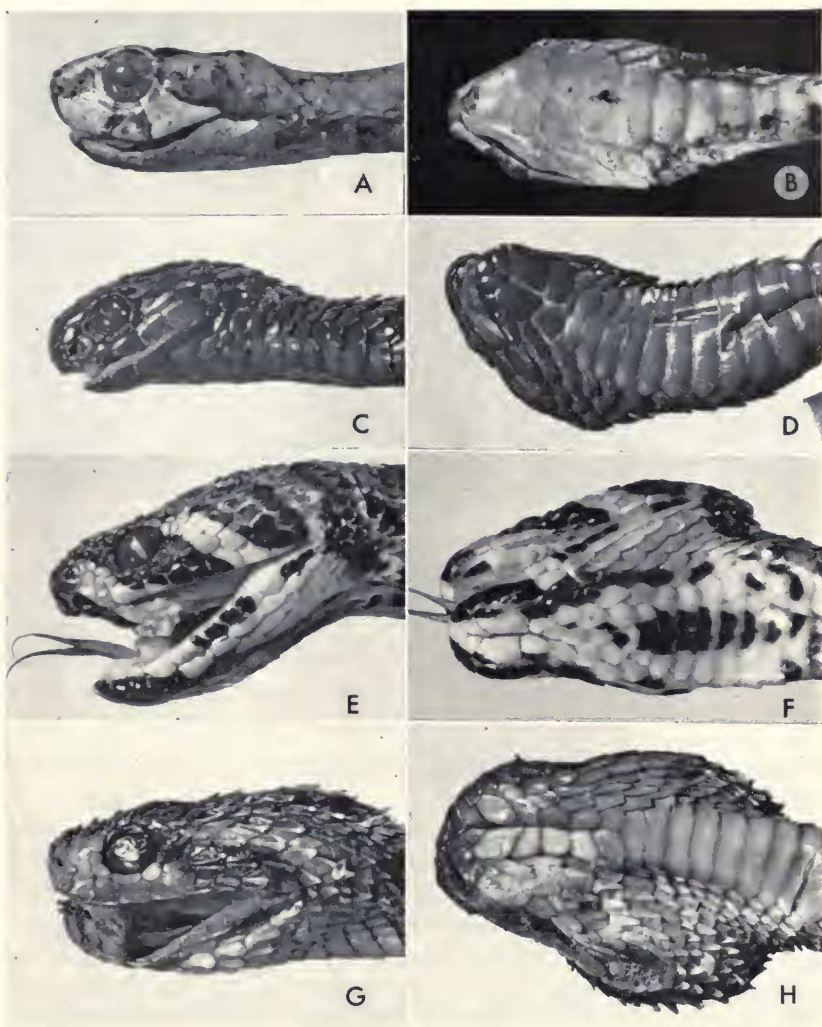
Fig. 41. A–B, *Haplopeltura boa* (CNHM 63602); C–D, *Adenorhinos barbouri* (Holotype); E–F, *Atheris superciliaris* (MCZ 30423); G–H, *Atheris squamiger* (CNHM 19481).

185

Adenorhinos, new genus

Subfamily assignment.—A viperid with small dorsal head scales, with the maxilla not hollowed out, and head lacking a loreal pit.

Generic diagnosis.—Dorsal head scales small and keeled, one anterior and one posterior smooth temporal (fig. 41, C), concave depression in posterior area of nasal scale (fig. 41, C); subcutaneous nasal gland.

↑
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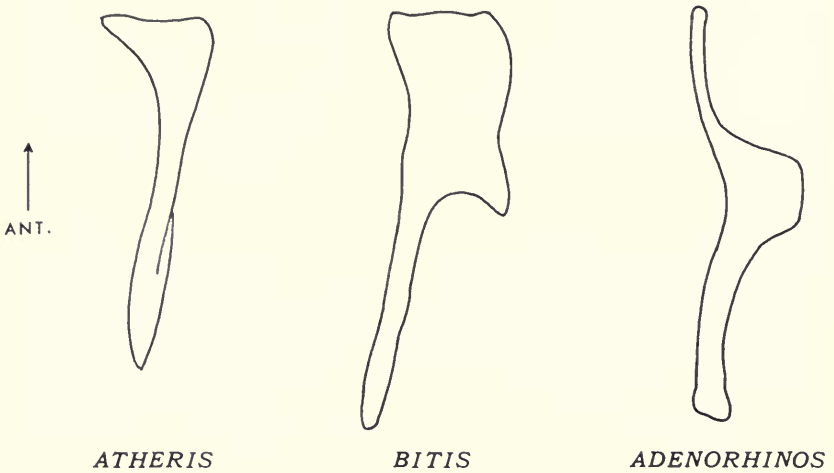
ATHERIS   BITIS   ADENORHINOS

FIG. 42. Ectopterygoids of *Atheris*, *Bitis*, and *Adenorhinos* (ventral view of the left ectopterygoid).

Generic description.—Skull: parietal bulbous laterally; distance between supratemporal and postorbital equal to inter-frontal suture; ectopterygoid with lateral flange without spine and with a long anterior process adjacent to the maxilla (fig. 42); postorbital long and narrow; parietal-postorbital suture: dorsally, suture is semi-circular and the parietal does not extend posterior to the postorbital, ventrally, parietal extends downward forming a triangular union with postorbital. Splenial absent, angular present. Head (fig. 41, C, D): top of head with small keeled scales; nasal single, nostril in extreme anterior area, posterior area having a depression, with a subcutaneous nasal gland; nasal in contact with first supralabial and preoculars and separated from rostral by one scale; eye very large, $1\frac{1}{2} \times$ distance to mouth, with vertical elliptical pupil, completely surrounded by ocular scales; subocular scales broadly in contact with three supralabials; temporals 1–1, enlarged and smooth; 5 to 6 smooth suprala-

Fig. 43. Skull of *Bitis arietans* (CNHM 11006).

bials; 5 smooth infralabials; 2 pairs of smooth chin shields with median groove; gulars smooth; anterior-most ventral in contact with posterior pair of chin shields. Dorsal scales imbricate and keeled, outermost row smooth; ventrals smooth; anal single; subcaudals smooth and single; long single terminal caudal scute.

Type species.—*Adenorhinos barbouri* (Loveridge).

Adenorhinos barbouri (Loveridge), new combination. Figures 41, C, D.

> *Atheris barbouri* Loveridge, 1930, Proc. New England Zool. Club, **11**, p. 107 —Dabaga, Uzungwe Mts., Tanganyika; 1933, Bull. Mus. Comp. Zool., **74**, p. 277; 1957, loc. cit., **117**, p. 305; Klemmer, 1963, Liste Gifts., p. 362.

Material examined.—MCZ 29055—holotype, MCZ 29056–57—paratypes, MCZ 30431, 30433–34; CNHM 142636 (ex. MCZ 30432).

Distribution.—Highlands of southern Tanganyika.

Since we have changed the taxonomic assignment of several species, we believe keys to the species of the following three genera and to the viperine genera incorporating our revisions of status will be useful.

KEY TO *BITIS, ATHERIS,* AND *ADENORHINOS*

1. Subcaudals single...2
   All or almost all subcaudals paired.................................8

2. Nasal in contact with rostral.........................*Bitis worthingtoni*
   Nasal not in contact with rostral....................................3
3. Nasal shield in contact with preocular (fig. 41, C, D)..*Adenorhinos barbouri*
   Nasal shield not in contact with preocular...........................4
4. Gulars smooth; keels of lateral scales serrated............*Atheris nitschei*
   Gulars keeled; keels of lateral scales without serrations.................5
5. Three enlarged scales separating the nasals............................6
   More than three subequal scales separating the nasals..................7
6. Eight or fewer scales separating eyes across top of head (figs. 41, G, H).
   Atheris hispida[1] and *Atheris squamiger*
   Ten or more scales separating eyes across top of head...*Atheris katangensis*
7. Two rows of scales separating eye from supralabials....*Atheris ceratophorus*
   Three rows of scales separating eye from supralabials......*Atheris chloroechis*
8. Nasal in contact with rostral; enlarged supraocular plate (fig. 41, E, F).
   Atheris superciliaris
   Nasal not in contact with rostral; supraocular region composed of numerous
   small scales...9
9. Nasal in contact with first supralabial ....*Atheris hindii*
   Nasal not in contact with first supralabial 10
10. Nasal separated from first supralabial by 4 or more scales..............11
    Nasal separated from first supralabial by 1 or 2 scales..................12
11. Supranasals: enlarged scales in contact with each other.......*Bitis gabonica*
    Supranasals: enlarged horn-like scales separated by small scales.
    Bitis nasicornis
12. Subcaudals keeled at least posteriorly..............................13
    Subcaudals smooth..15
13. Ventrals keeled.......................................*Bitis peringueyi*
    Ventrals smooth..14
14. Lateral scales smaller than dorsal scales and oblique...........*Bitis caudalis*
    Lateral scales subequal to dorsal scales and not oblique.........*Bitis cornuta*
15. Nasal separated from first supralabial by 2 scales............*Bitis heraldica*
    Nasal separated from first supralabial by 1 scale.....................16
16. Supranasals separated by 2 scale rows.....................*Bitis arietans*
    Supranasals separated by more than 2 scale rows.............*Bitis atropos*

[1] We have not examined the three known specimens of *Atheris hispidus* Laurent. Laurent (1956, p. 383) reported that *hispidus* differs from the sympatric specimens of the widely distributed *squamiger* in having fewer mid-body dorsal scale rows, fewer infralabials, and the type of keels on the scales of the neck.

Bitis inornata was unavailable for comparison. This rare form from extreme southern Africa may not be distinct. In his description of the species, Fitzsimons (1962, p. 346) stated that it appears "intermediate between *atropos* and *cornuta*."

KEY TO VIPERINE GENERA

1. Eye in contact with supralabials....................................2
   Eye not in contact with supralabials.................................3
2. Loreal present; pupil vertically elliptical.......................*Azemiops*
   Loreal absent; pupil round..................................*Atractaspis*

3. Three head shields across top of head between eyes.................*Causus*
   More than three head shields or scales across top of head between eyes....4

4. Ventrals keeled...5
   Ventrals smooth..7

5. Keels of lateral scales serrated................................*Cerastes*
   Keels of lateral scales not serrated.................................6

6. Subcaudals smooth...................................*Eristocophis*
   Subcaudals keeled...*Bitis*

7. Excavated nasal shield in contact with preoculars (fig. 41, C)...*Adenorhinos*
   Nasal shield not excavated and separated from preoculars by small scales
   (as in fig. 41, E)..8

8. Dorsal postorbital-parietal suture parallel to longitudinal head axis (as in
   fig. 33)..9
   Dorsal postorbital-parietal suture oblique to longitudinal head axis (as in
   fig. 32)...10

9. Supranasal sac present; ectopterygoid with lateral flange (figs. 42 and 43).
   Bitis
   No supranasal sac; ectopterygoid without lateral flange (fig. 42).....*Atheris*

10. Subcaudals single; keels of lateral scales serrated....................*Echis*
    Subcaudals paired; keels of lateral scales without serration...........*Vipera*

TABLE 9.—COMPARISON OF CERTAIN CHARACTERS OF ADVANCED ETHIOPIAN VIPERS

Character	Ectopterygoid Flange	Width of Postorbital	Supranasal Sac	Body Compressed	Subcaudals Paired	Scale Rows Between Nasal and	
						Rostral	First Supralabial
Bitis peringueyi	+	broad	+	0	+	2-3	1
Bitis caudalis	+	"	+	0	+	2	1
Bitis cornuta	+	"	+	0	+	2	1-2
Bitis atropos	+	"	+	0	+	2	1
Bitis heraldica	+	"	+	0	+	2	2
Bitis arietans	+	"	+	0	+	1-2	1
Bitis gabonica	+	"	+	0	+	4-5	4-5
Bitis nasicornis	+	"	+	0	+	5-6	4-6
Bitis worthingtoni	+	moderately broad	+	0	0	0	0
Adenorhinos barbouri	+	narrow	0	0	0	1	0
Atheris hindii	0	"	0	+/0*	+/0**	1	0
Atheris superciliaris	0	"	0	0	+	0	0
Atheris nitschei	0	"	0	+	0	1	0
Atheris katangensis	0	"	0	+	0	0	0
Atheris squamiger	0	"	0	+	0	1	0
Atheris chloroechis	0	"	0	+	0	1	0

* dorsum rounded, sides compressed

** CNHM 142082 has anterior subcaudals single

DISCUSSION OF PRIMITIVE CHARACTERS

Certain characters analyzed appear to reflect phylogenetic changes at the subfamily level and not merely specializations for particular modes of life.

Whether we assume that the viperids are derived from a generalized elapid stock, from an early colubrid group, or even from boids, those species with nine large head plates of the colubrid type (parietals, frontal, prefrontals, supraoculars, supranasals) are probably in the more primitive stocks. In *Vipera* a reduction of these large head plates to a condition of small keeled scales is accompanied by a greater number of scales between the eye and the supralabials and in a progressive reduction in size of the chin shields. The absence of large head plates is considered advanced in the other Palaearctic and Ethiopian genera. The large size of certain head scales in some *Atheris* and in *Adenorhinos* is probably a secondary development.

The parallel fragmentation of the head plates in viperines and crotalines suggests that it may have been an advantageous functional response to the development of large compact cephalic poison glands. In contrast, in some species of the vipers with colubrid head conformation (*Atractaspis* and *Causus*) enlarged venom glands are accommodated behind the head, as in the elapid genus *Maticora*. However, probably more important in the breakup of the primitive pattern of the head plates was the general widening and flattening of the roof of the skull in the advanced viperines and crotalines. Also, increased flexibility of the head skin may have been required anteriorly as the prefrontal bones became more involved in the fang-erection mechanism.

The splenial bone (fig. 34) is present in all the viperines with large head plates, in *Vipera*, and in *Eristocophis*. It is absent in *Echis*, *Cerastes*, and the three Ethiopian genera with small head scales. It is present in most families of snakes, including the Boidae, Colubridae, and Elapidae, and we therefore regard its absence as an advanced condition.

The possession of a movable prefrontal is shared by all viperids save *Azemiops*, *Causus*, and *Atractaspis*. A relatively inflexible joint between the prefrontal and frontal characterizes these three genera and the majority of colubrids and elapids. The full incorporation of the prefrontal into the fang-erecting mechanism is certainly to be regarded as an advanced condition in the viperids.

Of the three genera with large head plates, two (*Atractaspis* and *Causus*) are known to be oviparous. Information on the other, *Azemiops,* is lacking. Of the seven genera with variably reduced conditions of the head scales, two are known to be viviparous (*Bitis* and *Atheris*), three have intrageneric variation, in being oviparous and viviparous (*Vipera, Cerastes,* and *Echis;* Mendelssohn, 1963), and there is no certain information on the other two (*Eristocophis* and *Adenorhinos*). The viviparous condition is considered to be advanced.*

It therefore appears that the advanced conditions in the viperines are (1) small head scales, (2) absence of a splenial, (3) a prefrontal bone rotatable at its frontal joint, and (4) viviparous reproduction. *Bitis, Atheris,* and (presumably) *Adenorhinos* have all of these characteristics, whereas *Causus* and *Atractaspis* have none of them. *Azemiops* is like *Causus* and *Atractaspis* in regard to the morphological characters. *Vipera, Eristocophis, Echis,* and *Cerastes* are intermediate in respect to this set of characters, having the following combination of these characters: *Cerastes* and *Echis* 1, 2, 3; 4 variable; *Eristocophis* 1, 3 (no information on 4); *Vipera* 3; 1 and 4 variable.

Another osteological character that has been given great weight in our assessments of relationships is the nature of the postorbital support. In *Atractaspis* the postorbital bone is absent, a modification common in streamlining the skull for burrowing. In *Causus* and *Azemiops* the postorbital is a slender element simply attached to the parietal. In *Vipera, Eristocophis, Cerastes,* and *Echis,* the parietal has a lateral process that serves as a substantial bolster for the postorbital (as in fig. 32). In *Bitis* and *Atheris* this process is small and ventrally situated, and there is a broad dorsal junction of the two bones (as in fig. 33). *Adenorhinos* lacks the anterolateral process of the parietal, but has a somewhat complex articulation of the two bones.

ZOOGEOGRAPHY AND PHYLOGENY

Distribution.—The range of the subfamily Viperinae encompasses all of Africa and Eurasia, excluding extreme southeastern Asia. In addition, there are disjunct populations of *Vipera russelli* in eastern Java and the Lesser Sunda Islands. The Viperinae are sharply divided zoogeographically into genera restricted to the Ethiopian Region (*Atractaspis,* 16 species; *Causus,* 5; *Bitis,* 10; *Atheris,* 8; *Adenorhinos,* 1) and genera restricted to the Palaearctic Region

* The terms viviparous and ovoviviparous are here lumped under viviparous because definite information on the nature of the fetal-oviducal relations is lacking for most of the live-bearing species.

(*Azemiops*, 1; *Vipera*, 9; *Echis*, 2; *Cerastes*, 2; *Eristocophis*, 1). The only exceptions to these groupings are *Atractaspis engaddensis* from Sinai and Israel (Haas, 1950; Marx, 1952), and *Echis carinatus*, which ranges into the extreme northern limits of the Ethiopian Region (Loveridge, 1957). For distribution of individual genera, see Figures 44 and 45.

The distributions of *Atractaspis* and *Causus* are co-extensive, but the former is subterranean and thus ecologically segregated from the other vipers. *Azemiops* is known from a rather small mountainous area (Pope, 1935) from southeastern Tibet (Smith, 1943) to northern Burma and Indochina (Bourret, 1936).

The distributions of the advanced viperines form a remarkable zoned pattern. Except for *Eristocophis* and *Adenorhinos*, the ranges of the genera are extensive. In general, *Bitis* and *Atheris* are ecologically segregated in their broadly overlapping ranges. Their composite range is barely infringed upon by *Echis carinatus* of the basically Palaearctic *Vipera* group. The isolated populations of *Vipera russelli* in Java and the Lesser Sunda Islands are in dry, not humid tropical areas (Mertens, 1927; Kopstein, 1936).

Origin.—In the opinion of several workers, the idea of Boulenger (1896a) that the viperids arose from opisthoglyph colubrids is correct (Radovanovic, 1937; Anthony, 1955; H. M. Smith, 1952). Haas (1938, 1952) has favored an earlier, possibly aglyph colubrid, origin. However, other recent students of the question have supported Cope's (1896) proposition that the viperids came from a proteroglyph (elapid) stock (Bogert, 1943; Johnson, 1956; Dowling, 1959). We share the latter view.

In *Acanthophis*, a thick-bodied Australian elapid, there is a rather extraordinary parallel to the heavy-bodied viperid snakes. Its pupil shape and retinal anatomy (Walls, 1942), body musculature (Mosauer, 1935), partly rotatable maxilla-prefrontal complex (Kellaway, 1933), flanged ectopterygoid (CNHM 20769), scalation and habits, make it practically an advanced viperid of the *Agkistrodon-Bitis-Vipera* morphotype. Considering this example, it is not difficult to imagine the development of the various viperids from elapid stock.

A common stock for the viperid subfamilies is unquestionable in any case. However, the basic distinguishing feature of the crotalines, the loreal pit sense organ and the correlated excavation of the maxilla, is fully developed in all living forms, and thus far there are no annectant forms between the subfamilies known in the fossil record. Fossil remains are known in America of *Agkistrodon* and
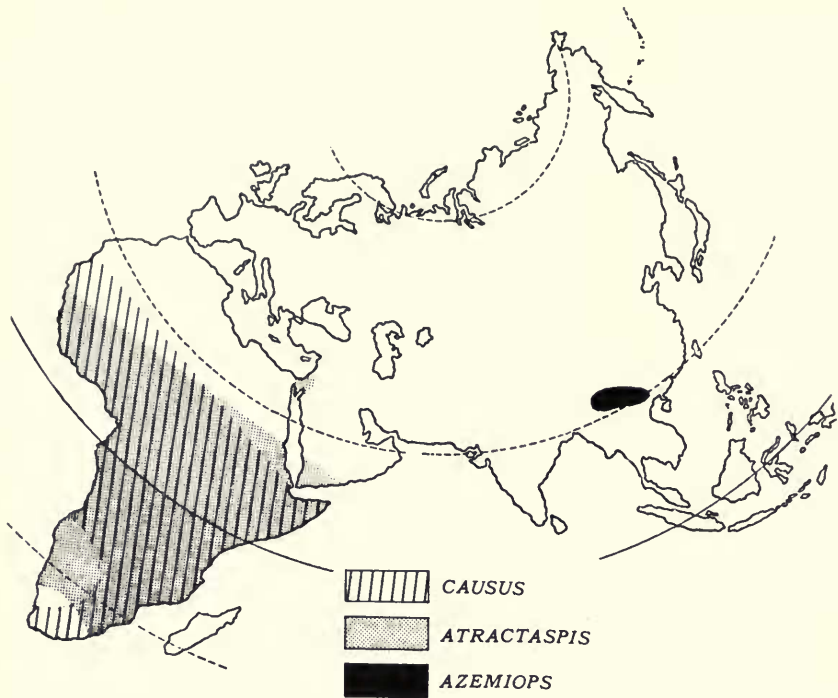
FIG. 44. Distribution of viperine genera with large head shields.

Crotalus from the Pliocene (Brattstrom, 1954). The oldest viperine fossil of which we are confident is *Vipera* from the Lower Pliocene of Europe (Bolkay, 1913, 1920).

Despite the loreal region specialization, the crotalines in part retain primitive conditions enumerated in the previous section for the viperines. The set of nine large dorsal head plates is found in *Agkistrodon* and *Sistrurus*. We examined several species and all genera of crotalines, and noted that the parietal has a process bolstering the postorbital in all, the splenial is present in all, and the short, distinctive prefrontal is apparently rotatable at its frontal joint in all. Oviparity occurs in species of eastern Asiatic *Agkistrodon* and *Trimeresurus* (Pope, 1935) and in *Lachesis muta* (Pope, 1944). Brattstrom (1964) concluded that *Lachesis* is probably a primitive survivor of the stock that gave rise to the rattlesnakes; he considered *Trimeresurus wagleri* and some of the Asiatic *Agkistrodon* to be the most primitive living pit-vipers. The multiplicity of elapids in the Australian region (24 of the 41 known genera are confined to this area—
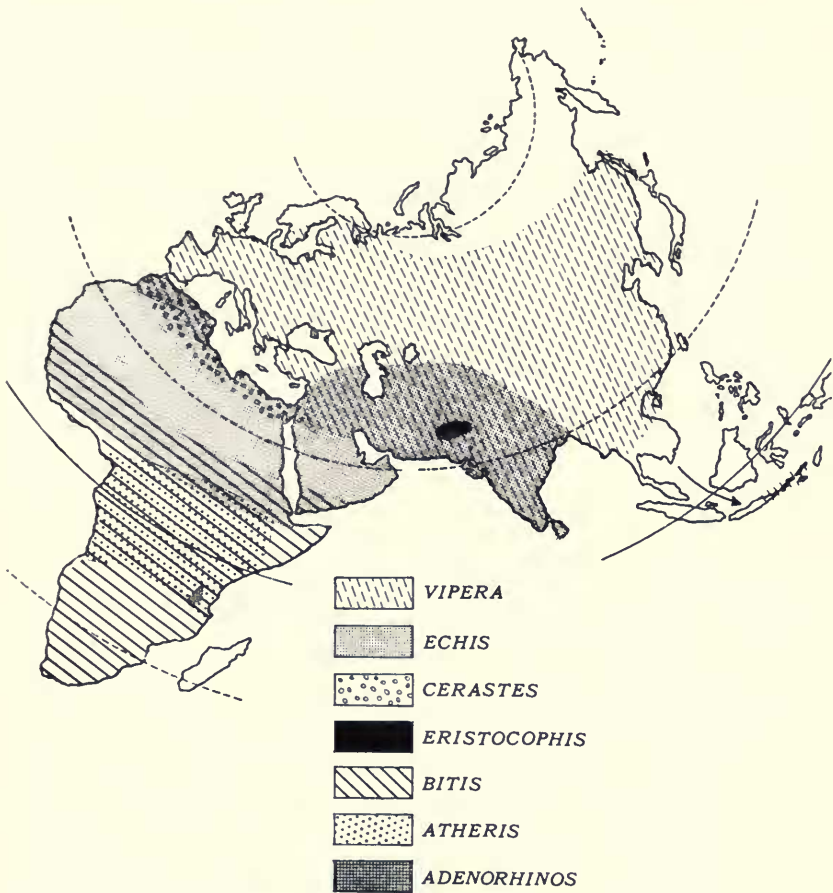
VIPERA

ECHIS

CERASTES

ERISTOCOPHIS

BITIS

ATHERIS

ADENORHINOS

Fig. 45.   Distribution of viperine genera with small head scales.

Klemmer, 1963), the Indo-Pacific distribution of their marine deriva-
tives, the Hydrophiidae, and the present distributions of the crota-
lines and viperines suggest an origin of the viperids in the Orient or
southeastern Palaearctic region.   The situation perhaps indicates
successive replacements or displacements of the hollow-fang groups
as they arose in this area.

Evidently an early radiation of the primitive erectile-fanged
snakes reached Africa and there survived in the flourishing, but
specialized, genera *Atractaspis* and *Causus*.   The slightly more ad-
vanced *Azemiops* inhabits a restricted upland area bordering the
Oriental region of today.   The advanced viperines presumably radi-
ated from a Palaearctic center, the crotalines from an Oriental one.

TABLE 10.—CLIMATIC CONDITIONS OF CERTAIN LOCALITIES IN SOUTHERN AND WESTERN ASIA, NORTHEASTERN AFRICA AND SOUTHWESTERN AFRICA*

Locality	Latitude	Longitude	Minimum mean monthly temperature, °C.	Mean annual precipitation, in mm.	Altitude, M.
WEST PAKISTAN: Kalat..............	29°02′N	66°35′E	2.9	244	2016.6
Quetta..............	30°11′N	67°00′E	3.2	220	1673.4
IRAQ: Basra..............	30°34′N	47°47′E	5.0	169	13.7
Khanaqin..............	34°18′N	45°26′E	9.4	314	202.1
EGYPT: Minya..............	28°05′N	30°44′E	11.8	6	40.4
Luxor..............	25°40′N	32°42′E	13.3	1	78.0
LIBYA: Sebha..............	27°01′N	14°26′E	12.1	308	444.1
ANGOLA: Vila Pereira d'Eca..............	17°14′S	15°44′E	16.8	666	1150.0
Mocamedes..............	15°12′S	12°09′E	16.5	51	0.0
BECHUANALAND: Maun..............	19°59′S	23°25′E	12.7	471	942.0
Mahalapye..............	23°04′S	26°48′E	13.3	454	1004.6
SOUTH WEST AFRICA: Windhoek..............	22°34′S	17°06′E	11.2	334	1727.0
Keetmanshoop..............	26°34′S	18°07′E	13.7	133	1066.0
SOUTH AFRICA: Ookiep..............	29°36′S	17°52′E	11.3	129	925.7

*1959. World Weather Records 1941–1950.

The alternative would be an African origin for the viperines. This appears less likely because of the specialized nature of the two primitive genera and the absence of any Ethiopian intermediates between them and the advanced *Bitis-Atheris* group. It is unlikely that *Vipera* or a similar advanced viperine stem stock would have completely died out in heterogeneous Africa if it had ever been there.

The morphological differentiation of the advanced viperines (and crotalines), the considerable radiation within the two main advanced viperine stocks, and the age of the fossils of the family assignable to present-day genera suggest a long history, probably dating back to the late Cretaceous. The morphological evidence suggests that the separation of the crotalines from the other viperids occurred after the differentiation of the stocks that gave rise to *Causus*, *Atractaspis*, and *Azemiops*. The crotalines appear closest to the *Vipera* group among all the viperines.

DISTRIBUTIONAL HISTORY

The history of the land masses is consonant with these ideas of origin and the present-day distributional picture of the viperines. From late Cretaceous until the Miocene the Tethys Sea formed a great variable barrier between Africa and Asia which would have separated the original, advanced viperine stock and allowed the subsequent separate development of the *Vipera* group and the *Bitis-Atheris* group (fig. 46). Presumably the distributional patterns of genera in other families also reflect this historical barrier. However, perhaps equally relevant to understanding of the distributions is an appreciation of the ecological aspects of the fauna and territory between the Oriental and Ethiopian regions.

What prevented the three Ethiopian stocks (*Atractaspis*, *Causus*, and *Bitis-Atheris-Adenorhinos*) and two Palaearctic stocks (*Azemiops* and *Vipera-Echis-Cerastes-Eristocophis*) from mixing after the disappearance of the Tethys Sea? *Echis carinatus* reaches arid Kenya and *Atractaspis engaddensis* reaches some oases of Sinai and Israel (see above). These are only two of over 50 species.

The first consideration is that temperature and/or humidity formed the barrier to inter-regional dispersal of these genera. This seems possible in the case of those taxa with restricted ranges, such as *Azemiops*, *Eristocophis*, and *Adenorhinos*. It may be true of *Atractaspis* to some degree since the isolated occurrence of *A. engaddensis* suggests contraction of a formerly more extensive range of the genus, leaving a relict in a restricted ecologically favorable area.

On the other hand, the Ethiopian *Bitis* is present in the tropical forests of Africa, the savanna, and in southern Africa, penetrating the most arid conditions of the deserts (Brain, 1960; see *Bitis* discussion, p. 181 this paper). Thus *Bitis* is capable of existing in various arid northern regions beyond its range. The reverse is true for the penetration of the Ethiopian Region by the vipers of Europe, Asia, and North Africa. Table 10 gives climatic data from southern and northern Africa and arid Asia. With regions having similar habitats, temperature, and humidity exploited by both stocks we reject temperatures or humidity as forming a major ecological barrier to the inter-regional dispersal of these stocks.

A further consideration is that the arid habitats were available for a long period. Schwarzbach (1946) reported desert formations in North Africa during the Eocene and Miocene (Moreau, 1952), and there is also evidence for similar conditions in central Asia for an extensive period of time (Suslov, 1961). Arid habitats are avail-
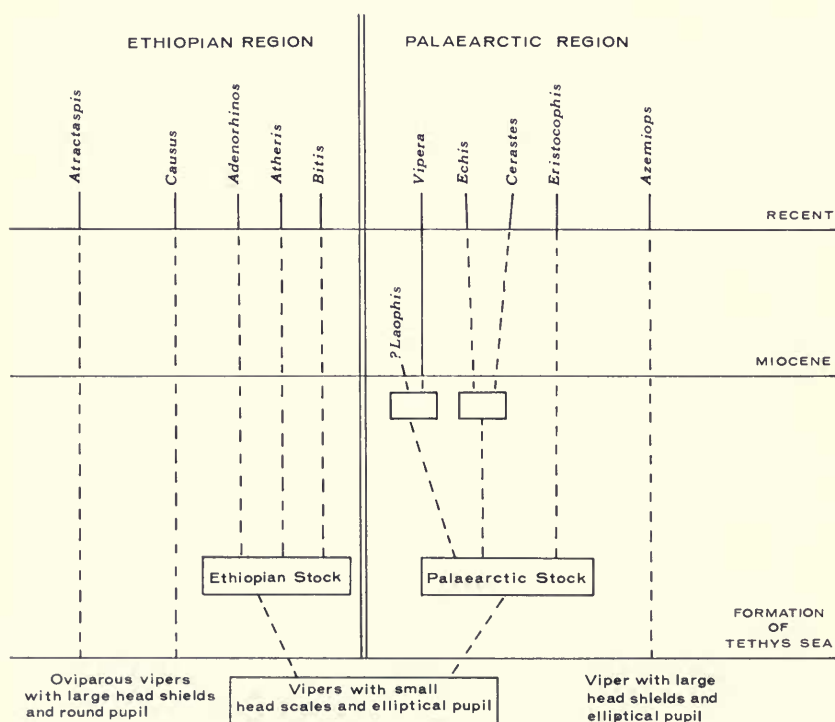

FIG. 46. Hypothetical phylogeny of viperid genera.

able in the Palaearctic Region today and are presently occupied by *Eristocophis, Cerastes, Echis*, and some *Vipera*.

Simple geographic separation is an alternative barrier. However, Africa, Europe, and Asia have been more or less a continuous land mass since the disappearance of the Tethys Sea in the Miocene (Moreau, 1952). Present day geography does not appear to be the barrier.

We believe the barrier to post-Miocene dispersal of the vipers was and is the presence of an ancient endemic fauna in each area. Previous to the Tethys Sea generalized stocks ranged the Afro-Eurasian lands and upon geographic fragmentation by the Tethys Sea they evolved separate stocks (fig. 46). Upon reconnection of these land masses the ecological niches and geographical areas were firmly occupied by their respective viperid faunas, which actually formed faunal barriers to each other. This zonal endemism is supported by the many genera of other snakes peculiar to central and southwestern Asia and northern Africa. The following non-viperid snake genera are almost exclusively restricted to the Palaearctic Region: *Sphalerosophis, Eirenis*, and *Lytorhynchus* (North Africa, Southwest Asia, and arid Pakistan and India), *Walterinnesia* (extreme northeast Africa and southwest Asia), *Malpolon* (North Africa, southwest Asia, and Europe), *Macroprotodon* (North Africa and Europe), *Rhynocalamus* (southwest Asia and southern Arabia), and *Coronella* (Europe). Only a single non-viperid species (*Typhlops braminus*—a cosmopolitan form) and very few genera are shared by the Ethiopian Region and the Oriental Region (Table 11). Obviously an intermediate faunal zone has formed a barrier for a long period and prevented the exchange of these two tropical snake faunas or their exchange with the Palaearctic fauna.

The present-day ranges of *Echis* and *Vipera* in the Oriental Region, the southern Saharan range of *Echis*, and the western part of the distribution of *Agkistrodon* presumably represent late Tertiary extensions from the centers of their stocks. The true vipers may have been separated from the pit vipers for most of their histories by the Uralian Sea and similar barriers.

CLASSIFICATION

Throughout the text we have referred all erectile-fanged snakes without loreal pits to the subfamily Viperinae. We have done so to conform to the almost universal present-day assignment of genera.

	Ethiopian		Arid Near Eastern			Western Oriental	Species Common to East Africa and India
	Belgian Congo[1] (64 genera)	East Africa[2] (54)	Egypt[3] (20)	Southwest Asia[4] (19)	West Pakistan[5] (26)	India & Adjacent Areas[6] (79)	
Typhlops	15 species	13	1	1	2	19	1*
Leptotyphlops	3	5	1	1	2	2	0
Python	2	1	0	0	1	2	0
Eryx	0	1	2	1	2	2	0
Lycophidion (?)	6	2	1?	0	0	0	0
Coluber	0	3	4	5	4	6	0
Boiga	2	2	0	0	1	13	0
Telescopus	1	2	2	5	1	1	0
Psammophis	4	5	3	1	3	5	0
Dasypeltis (?)	3	3	1?	0	0	0	0
Naja	3	2	2	0	1	3	0
Atractaspis	8	4	1	0	0	0	0
Vipera	0	0	0	2	1	2	0
Echis	0	1	2	1	1	1	1**

[1] deWitte, 1962
[2] Loveridge, 1957
[3] Marx, 1956
[4] Schmidt, 1939
[5] Minton, 1962
[6] Smith, M. A., 1943
* *Typhlops braminus*
** *Echis carinatus*

However, a truer reflection of our views involves resurrection of the group name Atractaspinae for *Atractaspis, Causus,* and *Azemiops.* A corollary is the maintenance of the pit-vipers as a subfamily of the Viperidae.

Summary

Over 260 specimens and 68 skulls of 43 species of viperine snakes were examined.   As a result, various reassignments of taxa were made.   *Pseudocerastes persicus* is considered a species of *Vipera;* the form *Pseudocerastes fieldi* is recognized as a subspecies of *V. persica,* and *P. bicornis* is synonymized with *V. p. persica.   Eristocophis* is a genus distinct from *Vipera* in several characteristics, including a paddle-shaped dorsal process of the premaxilla.   *Echis* and *Cerastes* are maintained as genera although their differentiation from each other is not so great as that of *Eristocophis* from *Vipera.*   These four Palaearctic genera are distinguished from the viviparous Ethiopian vipers by the nature of the postorbital bone and its articulation. On the basis of the form of the ectopterygoid and sundry external characters the advanced Ethiopian vipers are divided into three genera: *Bitis, Atheris,* and *Adenorhinos* (new genus for *A. barbouri*). The problematic forms *hindii* and *superciliaris* are considered terrestrial representatives of the predominantly arboreal genus *Atheris.* The fossil record of *Bitis* in the European Miocene is rejected.

Four characters are considered primitive in the family: the pattern of nine large dorsal head plates, presence of both splenial and angular elements of the mandible, a non-rotatable prefrontal bone, and oviparity.   On the basis of these characters *Causus, Atractaspis,* and *Azemiops* are clearly the most primitive genera in the family, whereas *Atheris, Bitis, Adenorhinos, Echis,* and *Cerastes* are advanced. *Vipera* and *Eristocophis* occupy an intermediate position.

The distributions of the Ethiopian and Palaearctic genera are practically mutually exclusive.   Judging from the morphological evidence accumulated by others, elapids are the group from which the erectile-fanged snakes arose.   The place of origin of the viperids appears to have been the Orient or the southeastern Palaearctic. *Atractaspis* and *Causus* represent a very early westward radiation of the vipers.   The separate development of advanced Ethiopian and Palaearctic viperine stocks is related to the barrier formed by the Tethys Sea.   The lack of inter-regional mixing of these stocks after the disappearance of the Tethys Sea in the Miocene is not due to

physical or ecological barriers but simply to the existence of the separate stocks themselves. The Palaearctic Region possesses a distinctive ophidian fauna that may have prevented exchange between the snake faunas of the Oriental and Ethiopian Regions.

REFERENCES

ANDERSON, S. C.
   1963.   Amphibians and reptiles from Iran.   Proc. Calif. Acad. Sci., **31**, pp. 417–498.

ANTHONY, J.
   1955.   Essai sur l'evolution anatomique de l'appareil venimeux des Ophidiens. Ann. Sci. Nat. (Zool.), **17** (11), pp. 7–53.

AUFFENBERG, WALTER
   1963.   The fossil snakes of Florida.   Tulane Stud. Zool., **10**, pp. 131–216.

BOGERT, C. M.
   1940.   Herpetological results of the Vernay Angola Expedition.   Bull. Amer. Mus. Nat. Hist., **77**, pp. 1–107.
   1943.   Dentitional phenomena in cobras and other elapids with notes on adaptive modifications of fangs.   Bull. Amer. Mus. Nat. Hist., **81**, pp. 285–360.

BOLKAY, ST. J. L.
   1913.   Adatok Magyarország Pannoniai és praeglaciális Herpetologiájához. Mitt. Jahrb. Ungar. Geol. Reichsanstalt, **21**, 16 pp.
   1920.   On the phylogenetical series *Vipera gedulyi* By.—*V. ammodytes* L.— *V. meridionalis* Blgr.   Sarajevo Glasn. Zem. Muz. Bosnia Herceg., **32**, pp. 1–12. [not seen]

BOULENGER, G. A.
   1896.   Catalogue of snakes in the British Museum (Natural History).   **3**, pp. 1–727.   London.
   1896a.   Remarks on the dentition of snakes and on the evolution of the poison-fangs.   Proc. Zool. Soc. London, **1896**, pp. 614–616.

BOURRET, RENÉ
   1936.   Les serpentes de l'Indochine.   **2**, pp. 1–505.   Toulouse.

BRAIN, C. K.
   1960.   Observations on the locomotion of the South West African adder, *Bitis peringueyi* (Boulenger), with speculations on the origin of sidewinding.   Ann. Transvaal Mus., **24**, pp. 19–24.

BRATTSTROM, B. H.
   1954.   The fossil pit-vipers (Reptilia: Crotalidae) of North America.   Trans. San Diego Soc. Nat. Hist., **12**, pp. 31–46.
   1964.   Evolution of the pit vipers.   Trans. San Diego Soc. Nat. Hist., **13**, pp. 185–268.

COPE, E. D.
   1892.   Remarks on the communication "Ein fossilier Giftzahn" *by* F. KINKELIN. Zool. Anz., **15**, p. 224.
   1896.   The classification of the Ophidia.   Trans. Amer. Philos. Soc., **18**, pp. 186–219.
   1900.   The crocodilians, lizards and snakes of North America.   Rept. U. S. Natl. Mus. for 1898, pp. 153–1270.

DE WITTE, G. F.
1962. Genera des serpents du Congo et du Ruanda-Urundi. Ann. Roy. Afr. Centr., Sci. Zool., (8) no. 104, pp. 1–203.

DOWLING, H. G.
1959. Classification of the Serpentes: a critical review. Copeia, 1959, pp. 38–52.

FITZSIMONS, V. F. M.
1962. Snakes of southern Africa. pp. 1–423. London, MacDonald.

FLOWER, S. S.
1930. The occurrence of *Pseudocerastes* in Sinai. Ann. Mag. Nat. Hist., (10) 6, p. 224.

HAAS, GEORG
1938. A note on the origin of solenoglyph snakes. Copeia, 1938, pp. 73–82.
1950. A new *Atractaspis* (mole viper) from Palestine. Copeia, 1950, pp. 52–53.
1952. The head muscles of the Genus *Causus* (Ophidia, Solenoglypha) and some remarks of the origin of the Solenoglypha. Proc. Zool. Soc. London, 122, pp. 573–592.

JOHNSON, R. G.
1956. The origin and evolution of the venomous snakes. Evolution, 10, pp. 56–65.

KELLAWAY, C. H.
1933. Some peculiarities of Australian snake venoms. Trans. Roy. Soc. Trop. Med., 27, pp. 9–34.

KINKELIN, FRIEDRICH
1892. Ein fossiler Giftzahn. Zool. Anz., 15, pp. 93–94.
1896. Ein fossiler Giftzahn aus den untermiocänen Hydrobienschichten von Hessler bei Mosbach-Biebrich. Abhandl. Senckenb. Natur. Ges., 20, pp. 36–49.

KLEMMER, KONRAD
1963. Liste der rezenten Giftschlangen Elapidae, Hydropheidae, Viperidae und Crotalidae. Die Giftschlangen der Erde. pp. 255–464. Marburg/Lahn, N. G. Elwert.

KOCHVA, ELASAR
1962. On the lateral musculature of the Solenoglypha with remarks on some other snakes. Jour. Morph., 110, pp. 227–284.

KOPSTEIN, FELIX
1936. Uber *Vipera russellii* von Java. Treubia, 15, pp. 259–264.

KRAMER, EUGEN
1961. Uber zwei afrikanische Zwergpuffottern, *Bitis hindii* (Boulenger, 1910) and *Bitis superciliaris* (Peters, 1854). Viert. Naturf. Ges. Zurich, 106, pp. 419–423.
1961a. Variation, Sexualdimorphism, Wachstum und Taxionomie von *Vipera ursinii* (Bonaparte, 1935) und *Vipera kaznakovi* Nikolskij, 1909. Rev. Suisse Zool., 68, pp. 627–725.

KRISHNA, DAYA and K. C. DAVE
1956. On the distribution of reptiles in the desert of Rajasthan. [abstract]. Proc. Indian Sci. Congr. Assoc. 43rd, 4, pp. 34–35.

LAURENT, RAYMOND

1950. Revision du genre *Atractaspis* A. Smith. Mem. Inst. Roy. Sci. Nat. Belgique, (2) **38**, pp. 1–49.

1956. Contribution a l'Herpétologie de la Region des Grandes Lacs de l'Afrique Centrale. I. Généralités II. Chéloniens III. Ophidiens. Ann. Mus. Roy. Congo Belge, (8) **48**: pp. 1–390.

LOVERIDGE, ARTHUR

1933. Report on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. VII Herpetology. Bull. Mus. Comp. Zool., **74**, pp. 195–416.

1942. Scientific results of a fourth expedition to forested areas in east and central Africa. IV Reptiles. Bull. Mus. Comp Zool., **91**, pp. 237–373.

1953. Zoological results of a fifth expedition to east Africa. III Reptiles from Nyasaland and Tete. Bull. Mus. Comp. Zool., **110**, pp. 143–322.

1955. On a second collection of reptiles and amphibians taken in Tanganyika Territory by C. J. P. Ionides, Esq. Jour. East Afr. Nat. Hist. Soc., **22**, pp. 168–198.

1957. Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). Bull. Mus. Comp. Zool., **117**, pp. 151–362.

LYNN, W. G.

1935. On the supranasal sac of the Viperinae. Copeia, **1935**, pp. 9–12.

MARX, HYMEN

1952. *Atractaspis* (mole viper), a new record for Egypt. Copeia, **1952**, pp. 278–279.

1956. Keys to the lizards and snakes of Egypt. U. S. Naval Med. Res. Unit No. 3, Research Report NM 005 050.39.45, pp. 1–8.

MENDELSSOHN, H.

1963. On the biology of the venomous snakes of Israel. Israel Jour. Zool., **12**, pp. 143–170.

MERTENS, ROBERT

1927. Zur Verbreitung der *Vipera russellii* Shaw. Senckenbergiana Biol., **9**, pp. 182–184.

MINTON, S. A.

1962. An annotated key to the amphibians and reptiles of Sind and Las Bela, West Pakistan. Amer. Mus. Nov., no. 2081, pp. 1–60.

MOREAU, R. E.

1952. Africa since the Mesozoic: with particular reference to certain biological problems. Proc. Zool. Soc. London, **121**, pp. 869–913.

MOSAUER, WALTER

1935. The myology of the trunk region of snakes and its significance for ophidian taxonomy and phylogeny. Publ. in Zool. Univ. Calif., **1**, pp. 1–120.

OWEN, R.

1857. On the fossil vertebrae of a serpent (*Laophis crotaloïdes*, Own.) discovered by Capt. Spratt, R.N., in a Tertiary formation at Salonica. Proc. Geol. Soc. London, **13**, pp. 196–199.

PARKER, H. W.

1932. Scientific results of the Cambridge Expedition to the east African lakes, 1930–1. 5. Reptiles and amphibians. Jour. Linn. Soc. London (Zool.), **38**, pp. 213–229.

1963. Snakes. 191 pp. New York.

PIVETEAU, JEAN
  1927. Etudes sur quelques amphibiens et reptiles fossiles. Ann. Palaeontologie,
    16, pp. 1–64.

POPE, C. H.
  1935. The Reptiles of China. Nat. Hist. Central Asia., 10, pp. 1–604.
  1944. Poisonous snakes of the New World. New York Zool. Soc., pp. 1–47.

RADOVANOVIC, M.
  1937. Osteologie des Schlangenkopfes. Jena Z. Naturw., 71, pp. 179–312.

SCHMIDT, K. P.
  1930. Reptiles of Marshall Field North Arabian Desert Expedition, 1927–1928.
    Field Mus. Nat. Hist., Zool. Ser., 17, pp. 223–230.
  1939. Reptiles and amphibians from southwestern Asia. Field Mus. Nat. Hist.,
    Zool. Ser., 24, pp. 49–92.

SCHWARZBACH, MARTIN
  1946. Klima und klimagurtel in Alttertiar. Die Naturwissensch., 33, pp. 355–
    361.

SMITH, H. M.
  1952. A revised arrangement of maxillary fangs of snakes. Turtox News, 30,
    5 pp.

SMITH, M. A.
  1943. The fauna of British India, Ceylon, and Burma. Reptilia and Amphibia,
    3, 583 pp.

SUSLOV, S. P.
  1961. Physical geography of Asiatic Russia. xiv + 594 pp. San Francisco.

U. S. WEATHER BUREAU
  1959. World Weather Records 1941–50. 1–1361 pp. Superintendent of Docu-
    ments, U. S. Govt. Printing Office.

WALL, FRANK
  1913. The poisonous terrestrial snakes of our British Indian Dominions (in-
    cluding Ceylon) and how to recognize them, with symptoms of snake poison-
    ing and treatment. Bombay.
  1928. op. cit., 4th ed., pp. 1–173.

WALLS, G. L.
  1942. The vertebrate eye and its adaptive radiation. Cranbrook Inst. Sci.
    Bull., no. 19, xiv + 785 pp.

WERNER, FRANZ
  1897. Ueber Reptilier und Batrachier aus Togoland, Kamerun und Tunis aus
    dem klg. Museum fur Naturkunde in Berlin. Verh. Zool. Bot. Ges. Wien,
    47, pp. 395–408.